REPRODUCTIVE BEHAVIOUR AND DEVELOPMENT OF THE DUNG BEETLE *TYPHAEUS TYPHOEUS* (COLEOPTERA, GEOTRUPIDAE)

by

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Abstract

This paper is part of a study of the contribution of dung beetles to soil formation in sandy soils. *Typhaeus typhoeus* (Linnaeus) has been selected because it makes deep burrows and is locally abundant. The beetles are active from autumn until spring, reproduction takes place from February to April. Sex pheromones probably influence pair formation. The sexes co-operate in excavating a burrow (up to 0.7 m below surface) and in provisioning the burrow with dung as food for the larvae. Co-operation is reset by scraping each other across the thorax or elytra. Dung sausages, appr. 12.5 cm long and 15 mm in diameter, are manufactured above each other. Development is rapid at 13—17 °C. The life cycle is accelerated by a cold period in the third larval stage. These requirements are met by soil temperatures up to 15 °C in summer and down to 5 °C in winter. The life cycle lasts two years, but longer under certain conditions. Newly hatched beetles make their way to the surface through the soil, but do not follow the old shaft. Adults reproduce only once. Differential rate of completion of the life cycle and occasional flying probably reduce the risk of local extinction. The study is thought to be relevant for behavioural ecology and soil science.

Contents

Introduction

There were two main reasons for this study of dung beetles. First, ancient traces of former activity by small burrowing or crawling animals, presumed to be dung beetles, can be found today in sandy soils. By studying the behaviour of dung beetles it should be possible to ascertain whether these are indeed the relics of dung beetle activity.

Second, in areas where dung beetles are abundant nowadays, recent traces of their activity are present in the soil and this raises the question of how much dung beetles contribute to soil formation today.

These topics will be discussed in subsequent articles. The ancient traces (with an account of their age) will be described in a forthcoming paper and will be compared with the traces resulting from recent dung beetle activity. It will be shown that dung beetles may indeed be responsible for the ancient traces.

Knowledge about the reproductive behaviour of the dung beetles is required for a proper understanding of their influence on soil morphology, and therefore this is discussed in the present paper. After a brief introduction to dung beetles as a group, the general biology of the species selected for study, i.e. *Typhaeus typhoeus* (Linnaeus, 1758), is described and its geographical range is discussed.

In order to quantify the beetles' contribution to soil formation it will eventually be necessary to explain and predict their population dynamics. This considerable task was reduced to two basic investigations in the present study. The first pertains to the development of life stages during the season and to phenological phenomena that seem to be related to the persistence of

the species in time and space. As this constitutes part of the biology of the species it has been included in the present paper. The second basic investigation pertains to the environmental conditions (including soil conditions) with which the beetles have to cope during the season of adult activity. These conditions may affect the beetles' burrowing and reproduction. This will be treated in another paper. It will be shown that the number of dung targets and their distribution in the field is of paramount importance for the population ecology of *T. typhoeus* and its impact on soil.

In its impact on soil *Typhaeus typhoeus* should serve as a model species for all Geotrupini found in the temperate Holarctic and, to some extent, also for other dung beetle species of the paracoprid type in other parts of the world.

Consequently, in this paper about *T. typhoeus*, the emphasis will be on aspects of behaviour that may help to explain the impact on soil formation caused by this kind of dung beetle. Aspects of the reproductive behaviour of *T. typhoeus* that have been published elsewhere will be re-described in terms of their relevance to soil formation. Furthermore, useful new information about behaviour and the development of life stages will be presented.

Dung beetles and their association with soil

Representatives of several coleopteran families are regularly found inhabiting dung, e.g., Hydrophilidae and Histeridae. The term "dung beetle", however, is usually restricted to a number of species belonging to the superfamily Scarabaeoidea. Scarab beetles, whether dung beetles or not, show a close connection with soil. The larvae of most species live underground on a food-stock of dung or plant remains, prepared by their parents, or they show a free-living, root-sucking habit. Adults of most species forage above-ground on fungi, dead organic matter or fresh leaves and burrow into the soil to prepare food-stocks for their larvae, to lay eggs or to hibernate or aestivate.

Living on dung may have evolved from living on dead organic matter and fungi (Iablokoff-Khnzorian, 1977; Crowson, 1981). In the family Geotrupidae, to which *Typhaeus typhoeus* belongs, all these habits occur and this family has been placed near the base of the scarabaeoid evolutionary tree by the authors mentioned above. Dung-feeding beetles may have developed the practice of digging into the soil as a result of searching for truffle-like fungi that adopted a subterranean life history during times of warming climate. The habit of making food-stocks out of dead organic matter or dung instead of searching for fungi is presumed to have developed subsequently.

Dung beetles spread all over the world from the Jurassic/Cretaceous periods onwards (Iablokoff-Khnzorian, 1977; Crowson, 1981). The Geotrupini tribe probably radiated out from the area of the Tertiary Tethys Sea (Krikken, 1980) and now shows a predominantly temperate, Holarctic distribution.

In addition to the Geotrupidae, one other family of scarab beetles is important for our study, viz., the Scarabaeidae. This family not only contains dung beetles (e.g. Scarabaeinae and Aphodiinae), but also beetles of the cockchafer type (Melolonthinae), which, as adults, live on fresh leaves and, as larvae, show a root-sucking way of live. Cockchafers will be discussed in a subsequent paper.

Choice of *Typhaeus typhoeus* as an object of study

The impact of dung beetles on soil may be two-fold: enrichment with dung or plant remains, and physical disturbance. On the basis of their impact on soil, dung beetles may be divided into three ecological groups, as proposed by Bornemissza (1969) in a different context.

First, the endocoprids, which pass their life cycle from egg to adult in the dung on the surface, or spend part of their life cycle a few centimetres deep in the soil, e.g. Scarabaeidae-Aphodiinae. Second, the telecoprids, which make a ball out of the dung, roll it some distance away and bury it superficially as a food source for the larva, e.g. Scarabaeidae-Scarabaeinae. And, third, the paracoprids, which burrow a fairly deep shaft under or close to the dung patch; part of the burrow is filled with food for the larvae and part of it is back-filled with soil, e.g. Geotrupidae.

Because of the depth of the shafts and the amount of dung transported below the ground, dung beetles of the paracoprid type, especially the larger species, may be considered to have the greatest impact on soil. In the temperate regions, paracoprid dung beetles of the Geotrupini tribe are the most important in this respect, as has been shown by the studies of Fabre (± 1910), Schreiner (1906), Spaney (1910), Von Lengerken (1954), Howden (1955, 1964, 1974),

Table 1. Depth of shafts in Geotrupidae.

faunal region	species	depth of shaft (cm)	source
Palaearctic	*Geotrupes mutator**	≦ 30	Teichert, 1955
	*G. spiniger**	25— 30	Lumaret, 1980
	*G. stercorarius**	≦ 50	Teichert, 1955
		35— 60	Spaney, 1911
	*G. stercorosus**	35— 60	Spaney, 1910
	*G. vernalis**	12— 68	Teichert, 1959a
	Lethrus apterus	60—100	Frantsevich et al., 1977
		75—100	Teichert, 1959b
		50— 65	Schreiner, 1906
	Typhaeus momus	10— 15	Baraud, 1977
	*T. typhoeus**	29—100	present study
		60—100 (150)	Kuyten, 1960
		48—130	Teichert, 1959b
		70—140	Spaney, 1910
		≦ 150	Fabre, ca. 1910
	T. hiostius	60—160	Crovetti, 1971
Nearctic	*Geotrupes egeriei*	20— 75 (90)	Howden, 1955
	G. hornii	40— 75	id.
	Bolboceras farctum	57	id.
	Bradycinetulus ferrugineus	35—105	id.
	Mycotrupes retusus	45— 90	Olson, Hubbell & Howden, 1954
	M. gaigei	≦ 205	id.
	Peltotrupes youngi	140—270	Howden, 1952

* occurring in The Netherlands.

Teichert (1955, 1956, 1957, 1959a), Kuijten (1960), Crovetti (1971) and Klemperer (1978, 1979). There are differences between geotrupid species in, for example, geographical range, habitat, (use of) flight capability, reproductive season, depth of the shaft (table 1) and number of eggs laid (table 2).

In northwest Europe, *Typhaeus typhoeus* (fig. 1) is one of the most obvious species to study. The beetles are locally abundant with a maximum of 1—2 pairs per m² and they make very deep burrows (tables 1 and 3). Occasionally I have found them as deep as 1 m and they may go even deeper, up to 1.50 m (Fabre, ± 1910; Spaney, 1910; Teichert, 1959b; Kuijten, 1960). Moreover, they transport a fair amount of dung below the ground, as reflected by the number of dung sausages produced (= number of eggs laid; tables 2 and 4).
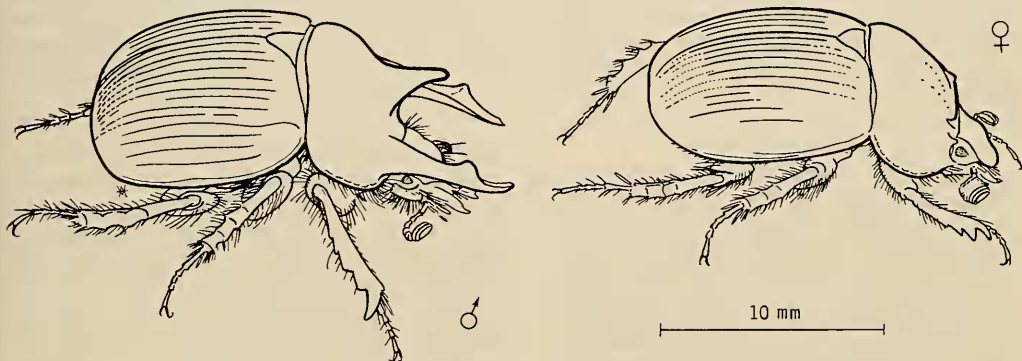

Fig. 1. *Typhaeus typhoeus* (Linnaeus, 1758). Left, male, and right, female.

Table 2. Number of eggs laid per nest or per female (if reported) in Geotrupidae.

species	number of eggs laid per nest or per female	source
*Geotrupes mutator**	4—16 per ♀	Teichert, 1955
*G. spiniger**	9—10 per ♀	Lumaret, 1980
*G. stercorarius**	4—17 per ♀	Teichert, 1955
	(2) 3— 6 (8)	Spaney, 1910
*G. vernalis**	5—10 per ♀	Teichert, 1959a
Lethrus apterus	5— 7	Frantsevich et al., 1977
	6—11 per ♀	Schreiner, 1906
*Typhaeus typhoeus**	(1) 4—16 (21) per ♀	present study
	1— 6 per nest (field)	id.
	≦ 10 per nest	Palmer, 1978
	≦ 15 per ♀	Kuyten, 1960
	3— 6 (8)	Spaney, 1910
T. hiostius	2— 8 per nest (field)	Crovetti, 1971

* occurring in The Netherlands.

General biology

Nesting

The reproductive behaviour consists of burrowing a branching shaft, provisioning the branches with food for the larvae and sealing the remaining burrow partly or completely with soil. Though the female, once fertilized, can perform the whole process on her own, the beetles normally operate in pairs. Some aspects of the reproductive behaviour have been outlined previously by Fabre (± 1910), Kuyten (1960) and Palmer (1978).

Habitat

The habitat is open to half open heathland, and the beetles are most abundant in bare areas surrounded by *Nardus stricta*, *Cladonia* spp. and *Calluna vulgaris*, and along paths. They also occur in open pine woods, predominantly along paths and in small clearings. A vital prerequisite is the presence of dung. The beetles are found only on herbivore dung, mostly that of rabbits, as the rabbit is the most abundant herbivore in the habitat of *T. typhoeus*. They will also use dung from sheep, deer and roe.

Seasonal and diurnal incidence

From the second half of September onwards and throughout the winter, *T. typhoeus* is active whenever the temperature is above zero and there is no snow. Intense activity occurs in October and November, which is the main period of maturation feeding, and from February to April, which is the main period of reproduction. From May onwards the reproductive activity declines rapidly and from June to the latter half of September there is no adult activity at the soil surface (fig. 2). Contrary to the common assumption that the beetles only reproduce after the turn of the year (Fabre, ± 1910; Main, 1917; Kuijten, 1960) I have established from field observations that pair formation, oviposition and provisioning with dung is not exceptional as early as the third week of October. On the other hand, unpaired beetles can be found in shallow burrows as late as March, where they are apparently still involved in maturation feeding.

Although in overcast and humid weather activity on the surface by day is not exceptional, *T. typhoeus* is usually active above-ground at dusk and at night.

Distribution

The genus *Typhaeus*

The genus *Typhaeus* Leach, 1815, contains six species of about the same size: 14—22 mm long and 8—11 mm wide. Five of these are restricted to the Mediterranean area: *T. hiostius* (Gené, 1836), *T. momus* (Olivier, 1789), *T. fossor* (Waltl, 1838), *T. lateridens* (Guérin, 1838) and *T. typhoeoides* Fairmaire, 1852. The first of these is endemic to Sardinia. The sixth species, *T. typhoeus* has the largest geographical range: from Morocco to South Sweden, westwards to Ireland and eastwards to Poland (Horion, 1958; Lindroth, 1960) and Yugoslavia (Miksič, 1956), but it is absent in Hungary (pers. obs. and Endrödi, pers. comm., 1981). A preliminary map of the distribution in Europe is given in fig. 3.
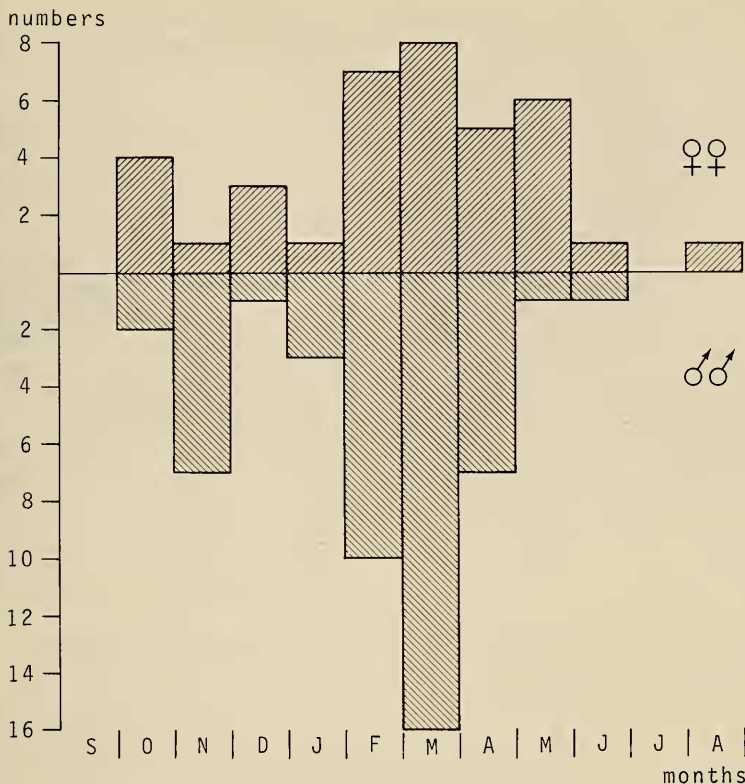
Fig. 2. Number of *Typhaeus typhoeus* captured in standard pitfalls in various heathlands in the Dutch province of Drenthe during the years 1959—1967. (Courtesy of P. J. den Boer.)

Typhaeus typhoeus in The Netherlands

In The Netherlands, *T. typhoeus* is found in sandy areas, even in isolated spots surrounded by peat, clay or loam soils (Gaasterland, Betuwe, South Limburg) but, remarkably, it is not present in the dunes along the west coast and on the Wadden islands in the north of the country. Fig. 4 is a preliminary map of the distribution of *T. typhoeus* in The Netherlands.

Absence from the dune region

In a preliminary experiment to ascertain the reasons for the absence of *T. typhoeus* from the dunes, it was found that under laboratory conditions two pairs of beetles reproduced quite normally when supplied with pellets of rabbit dung from the Wadden island of Vlieland. The trial was stopped when the larvae were in their final instar. Under field conditions in enclosures in the dunes of North Holland near Castricum, beetles made normal burrows in which they provisioned dung for their offspring, whether supplied with pellets of rabbit dung from the dunes (two pairs) or from the inland (two pairs). When the burrows were excavated six months later, it appeared, however, that only one of the 22 dung sausages contained a live larva, whereas in most of the other cases the larva had died and in some cases the egg had evidently not hatched. This work needs to be continued to yield conclusive results.

METHODS

To study the behaviour of *T. typhoeus* in the laboratory, the beetles were kept in cages (1 m high and 0.60 m wide), similar to the one described by Main (1916/17): a wooden frame in which two windows (4 mm thick) were kept a distance of 15 mm (sometimes 12 mm) apart. The space between the windows was filled from above with tamped down portions of sand that came from a field at Wijster, in the Dutch prov-
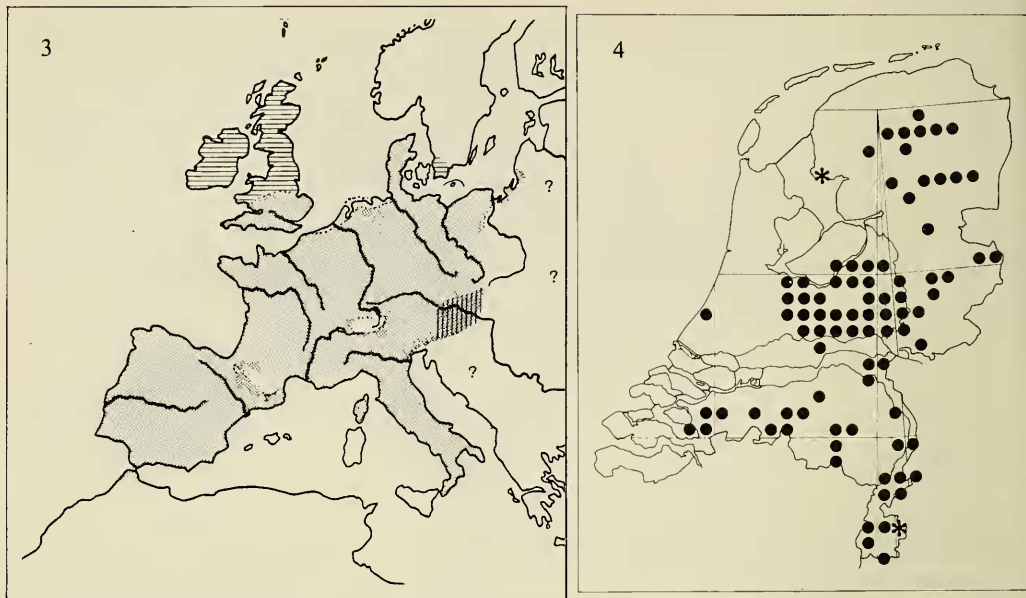
Fig. 3. Geographical range of *Typhaeus typhoeus*. Grey area: after Pijpers (1981). Striped area: *typhoeus* present according to Horion (1958), Lindroth (1960) and Sinclair (1977). Barred area: *typhoeus* not occurring according to Endrödi (pers. comm., 1981).

Fig. 4. Distribution of *Typhaeus typhoeus* in The Netherlands. After Pijpers (1981). Each dot indicates at least one specimen. Stars constitute additional occurrences, assessed by present author. The dot near the west coast pertains to two specimens, captured around the turn of the century.

ince of Drenthe, where *T. typhoeus* occurs naturally. The soil there is coversand to a depth of 1.40 m, in which a podzol has developed (Van Heuveln, 1965). The predominant particle size was 0.1—0.2 mm and particles larger than 0.6 mm were scarce. The organic matter content of the sub-soil was 0.6%. The sand was air-dried and subsequently moistened to a water content of 10% (by mass) to approximate field conditions in September at a depth of about 0.50 m below the surface. The tamping resulted in a bulk density of approximately 1.50 g/cm³, which was similar to the field situation at about 0.50 m below the soil surface.

The beetles made their burrows in the sand between the windows. The light/dark regime in the rooms with the cages was the same as in nature. Daylight conditions were simulated with TL-33 tubes supplemented with normal bulbs. To prevent light affecting the beetles in the soil, the windows of the cages were covered with sheets of black plastic. A horizontal walking-surface (0.50 × 0.60 m²) on which dung could

be offered was mounted on top of the glass cage and covered with 0.8 mm mesh wire-netting to prevent the beetles from flying away. Observations were usually carried out under dim red light, after the plastic sheets had been removed.

For the rearing 60 cages were used. To compare the laboratory results with the field situation, five cages were dug into the soil in the field at Wijster. In addition, the experimental equipment in the field included five 1 × 1 m² and six 2 × 2 m² enclosures consisting of 0.50 m wide stainless steel plates which were inserted to a depth of 0.20 m in the soil. These enclosures were also spanned with the wire-netting.

Almost all beetles used in the experiments were captured at the same site near Havelte in the province of Drenthe. Newly hatched adults can easily be collected in autumn from under the small hummocks of soil, where they have retired with some dung for their maturation feeding. Prior to experiments the beetles were kept in sand-filled plastic jars, 13 cm high and 10 cm in diameter, for a least six weeks at 5 °C.

Further details about the experimental methods will be given in the appropriate sections below.

REPRODUCTIVE BEHAVIOUR

Emergence and maturation feeding

The first newly hatched adults of *T. typhoeus* appear on the surface in the second half of September, usually after heavy rain. They immediately go in search of dung.

As soon as a beetle has found a small collection of dung it excavates a J-shaped feeding burrow approximately 15—20 cm deep (in the case of females sometimes deeper) and 13—16 mm in diameter. The beetle carries a number of dung pellets (in the case of rabbit dung mostly 10—20) down into its burrow and starts its maturation feeding. Given that reproduction was observed as early as the third week of October, the maturation feeding time in *T. typhoeus* is probably approximately four weeks, at a temperature of 13—16 °C.

Flying

To judge from the many beetles I found crawling around on the surface and the relatively few flying, it would seem that the beetles mostly move by walking and less so on the wing. Nonetheless, flying was observed in the field at a temperature of about 12 °C in the second week of October at dusk, in foggy weather with little wind. The beetles emerged from their burrows with their hind wings already unfolded and pumped up and flew off immediately. They flew low, zigzagging over the vegetation and the maximum distance I saw covered in one

flight did not exceed an estimated 50 m. Attempts to fly were also observed at the same time of the day in the laboratory in the plastic jars in which the beetles were kept prior to experiments. Blut (1938) encountered *T. typhoeus* flying at dusk in late May. Flying is possible even at very low temperatures, since in one of my laboratory experiments a female flew around in the walking area of a glass cage at 5 °C, although she had been subjected to that temperature for over six weeks.

To study flight movements in *T. typhoeus* more closely, two window traps and a mist-net trap were placed in a study plot at Wijster, in the Dutch province of Drenthe. The window of the window trap measures 100×50 cm² and it catches beetles flying at a height of 150—200 cm above the ground. The mist-net trap measures 100×50 cm², catching beetles flying 20—70 cm above the ground. After colliding with a trap the beetle falls down into a reservoir containing 4% formaline. The two window traps were in operation from 29 September 1978 and the mist-net trap from 8 November 1978 until the summer of 1980. In all, 19 beetles were trapped: eight males and eleven females (fig. 5). Fifteen beetles were captured in the single mist-net trap and only four in the two window traps, which confirms that the beetles fly low. Of the eleven females, ten were relatively unimpaired when the trap was inspected; two (captured on 27 September and 1 October, respectively) showed developing ovaries and had not yet mated; eight contained eggs and had mated, to judge from the presence of sperm cells. This shows that although no flying beetles were captured during peak reproduction in March, *T. typhoeus* can be
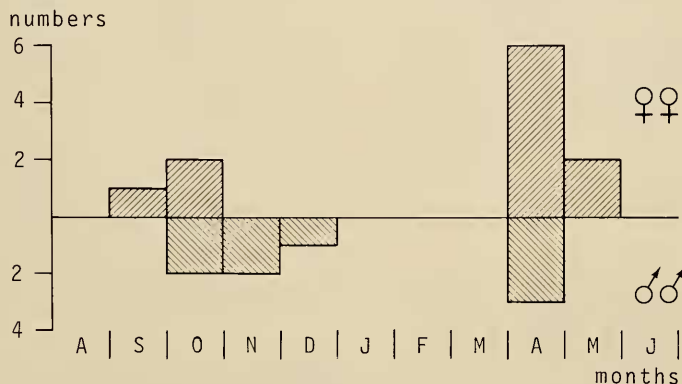

Fig. 5. Number of beetles trapped in flight at a study plot at Wijster (province of Drenthe, The Netherlands) during 1978/79 and 1979/80.
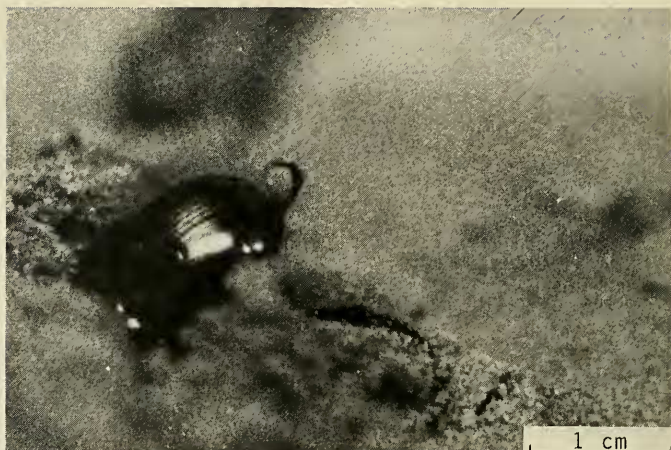
Fig. 6. Stance adopted by male *Typhaeus typhoeus* for supposed pheromone release during defecation. (Photo of beetle in nest entrance on walking surface of glass cage.)
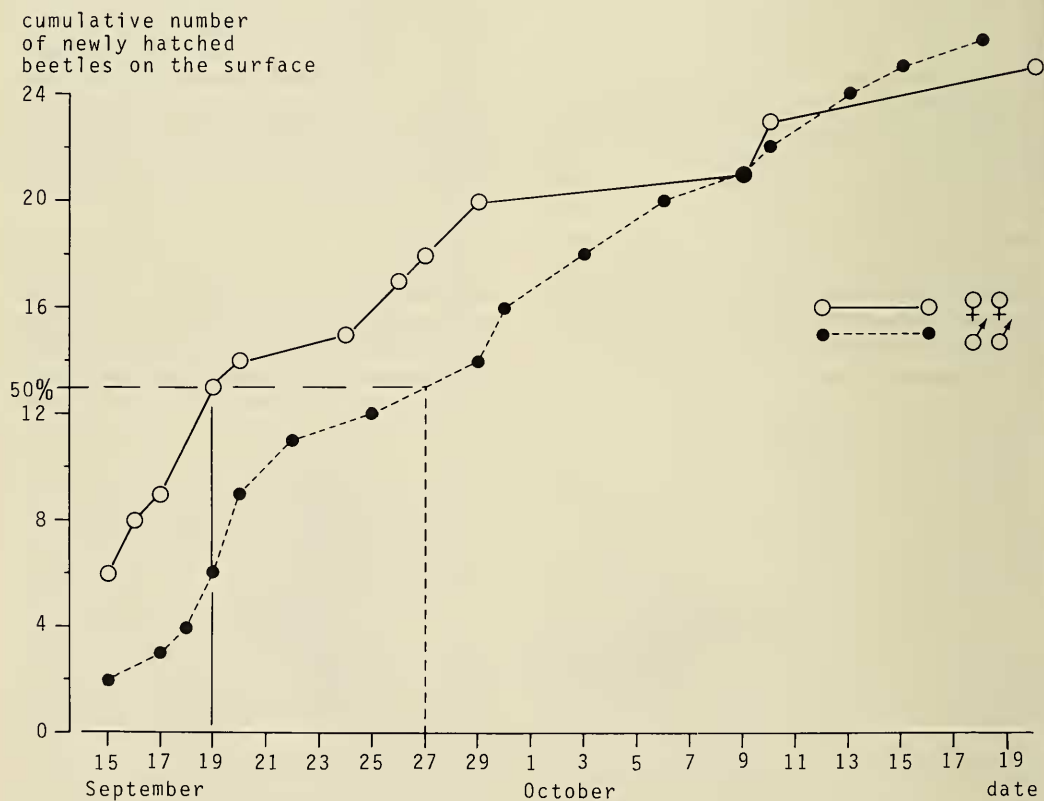

Fig. 7. Cumulative number of newly hatched male and female beetles appearing at the surface in September and October 1980 in a rearing trial started in late winter 1979.

added to the list of species not obeying the oo-genesis-flight syndrome of Johnson (1969).

The gut content of 14 of the trapped beetles was qualitatively estimated. In five beetles the gut was half filled or less, in nine the gut was more than half full. From these findings it cannot be concluded that a shortage of dung is the reason for flight.

Settlement and pair formation

Crovetti (1971) states that in *Typhaeus hiostius* the male penetrates the feeding burrow of a female after maturation feeding. In *T. typhoeus* I have observed behaviour that strongly suggests that pheromones may play a role, at least

in some stage of adult life, in pair formation: under laboratory conditions I have repeatedly observed that a male who has abandoned a nest with a female, then digs a shallow burrow near a food source, similar to the J-shaped feeding burrow. Next to this the male can be observed defecating in a characteristic stance, his body tilted at an angle of about 45° to the surface with his head above the entrance of the burrow and his abdomen lifted (fig. 6). This stance suggests that a pheromone is released with the excrement. Although the hypothesis of pheromone release needs experimental confirmation, it is significant that this stance was invariably adopted around the time that the light in the ex-
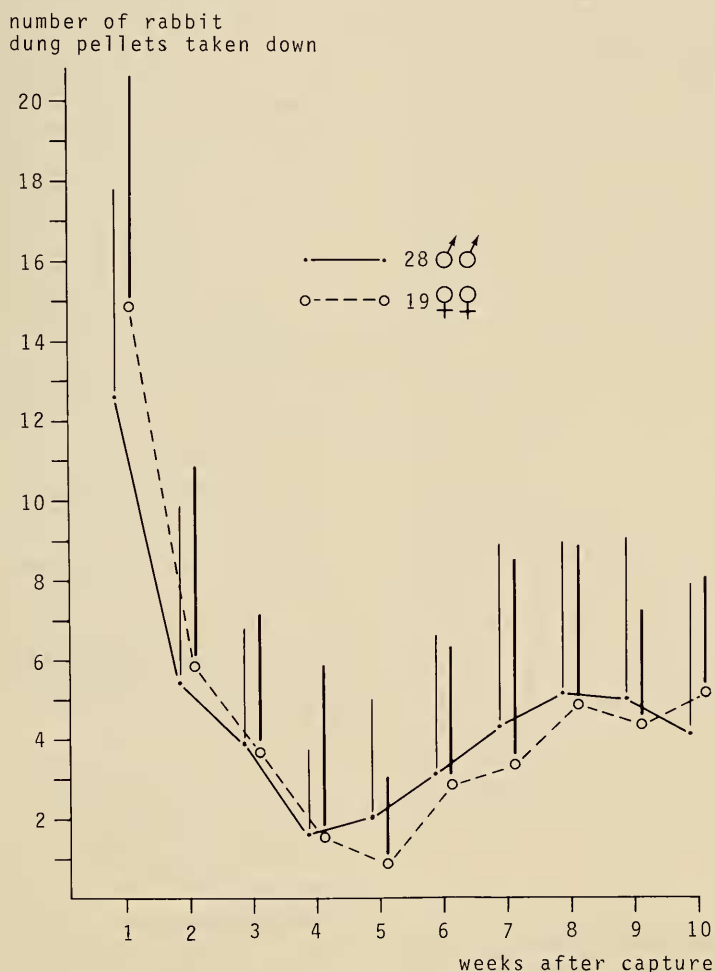

Fig. 8. Mean number of rabbit dung pellets carried down by beetles kept in plastic jars at 13—16 °C for ten weeks after their capture on 29 September and 4 October 1978. Vertical lines indicate upper half of standard deviation.

perimental room was automatically switched on or off, i.e., around dawn or dusk. At those times the weather is usually favourable for odour communication because of high air humidity and moderate wind velocity.

Crovetti's (1971) observation that the male joins the female after maturation feeding and my observation that males appear to be trying to attract females after the pair has split up, suggests that the former behaviour changes to the latter in the course of the season (assuming the two *Typhaeus* spp. behave similarly). There is some evidence to support this. In the rearing trials I carried out, the females usually appeared on the surface and started maturation feeding before the males: the median of the total number of females on the surface was reached eight days before that of males (fig. 7). Furthermore, in a cohort of beetles captured in the field, females carried down the same quantity of dung for maturation feeding as did the males (fig. 8). If the duration of maturation feeding is the same for both sexes then it seems probable that females mature sexually earlier than the males. For a female, the prerequisites for reproduction are a male and an adequate amount of dung, as a food source for the future larvae, and therefore her most profitable strategy seems to be not to go and search for one of the few males available for mating, but rather to settle near a spot rich in dung, make a shallow burrow and wait there for a male. This needs to be confirmed by additional research.

During the reproductive season the pattern changes: whenever a pair of beetles abandons a nest it is usually the male who leaves first, as will be reported in greater detail in another paper. Several days may pass before the female appears outside the burrow. By the time the male leaves the burrow most females will be paired and involved in breeding, so that it is unprofitable for him to search for one of the few burrows with an unpaired female. Instead, he seeks a spot with plenty of food, near which a new nest can be made, and tries to attract one of the females that will appear above-ground after abandoning a nest.

Copulation

On the first encounter, which usually takes place in a shallow feeding burrow, the male vigorously sweeps his front tibiae across the female's thorax, the female turns around and then the male sweeps across her elytra while half mounted on her back. Finally, the female lifts her abdomen and copulation follows, lasting from 3 to 20 min. The female terminates the copulation by stepping forwards a few cm, turning around and pushing the male back.

Burrowing

Having paired and copulated the beetles make a nest that finally consists of a shaft that may or may not divide into tunnels, from which a number of brood chambers branch off, provisioned with dung for the progeny and sealed by backfilling with soil (fig. 9). The female excavates by scraping the sand under her body with her front tibiae and then using her middle and hind legs to move it further back. As the sternites are densely covered with backward-pointing hairs, the sand does not fall down past the beetle when she is in a vertical position. While excavating, the beetle intermittently turns around its length axis. Every time the beetle has excavated 0.5—1.0 cm of the shaft she moves several mm backwards, and by doing this tamps down the moist sand behind her into a plug. Then she turns around and pushes the plug into the shaft with her head and thorax, again intermittently turning around her length axis. This turning enables her to apply force to a different point and thus facilitates the transport of the plug. The upper part of the shaft, within a depth of 30 cm from the surface, is made horizontal for some 10—15 cm (fig. 9). Here the female always leaves her sand plug before returning down the burrow to continue excavating. The male then burrows through the sand plug. Since the female has left the plug in a horizontal part of the passage, the sand does not fall down the shaft. Once past the small plug, the male turns around and shovels it to the exit, transporting it in the same way as the female. In this way a sand heap gradually accumulates on the surface, finally achieving a height of some 5 cm and a diameter of 10—15 cm.

In one of the glass cages the excavation of the shaft was closely monitored. Fig. 10 clearly shows that the beetles may continue to excavate for four days without pausing.

On four successive days, during periods indicated in fig. 10, I recorded the intervals during which the female was involved in sand excavation and transport, respectively. On the first three days the duration of the periods of excavation was the same, on the fourth day the duration was much longer, presumably indicating that the female was about to terminate the bur-

depth(cm)

store room →

shaft

path followed by emerging beetle

← tunnel

← sealing sand

dung sausage in brood chamber
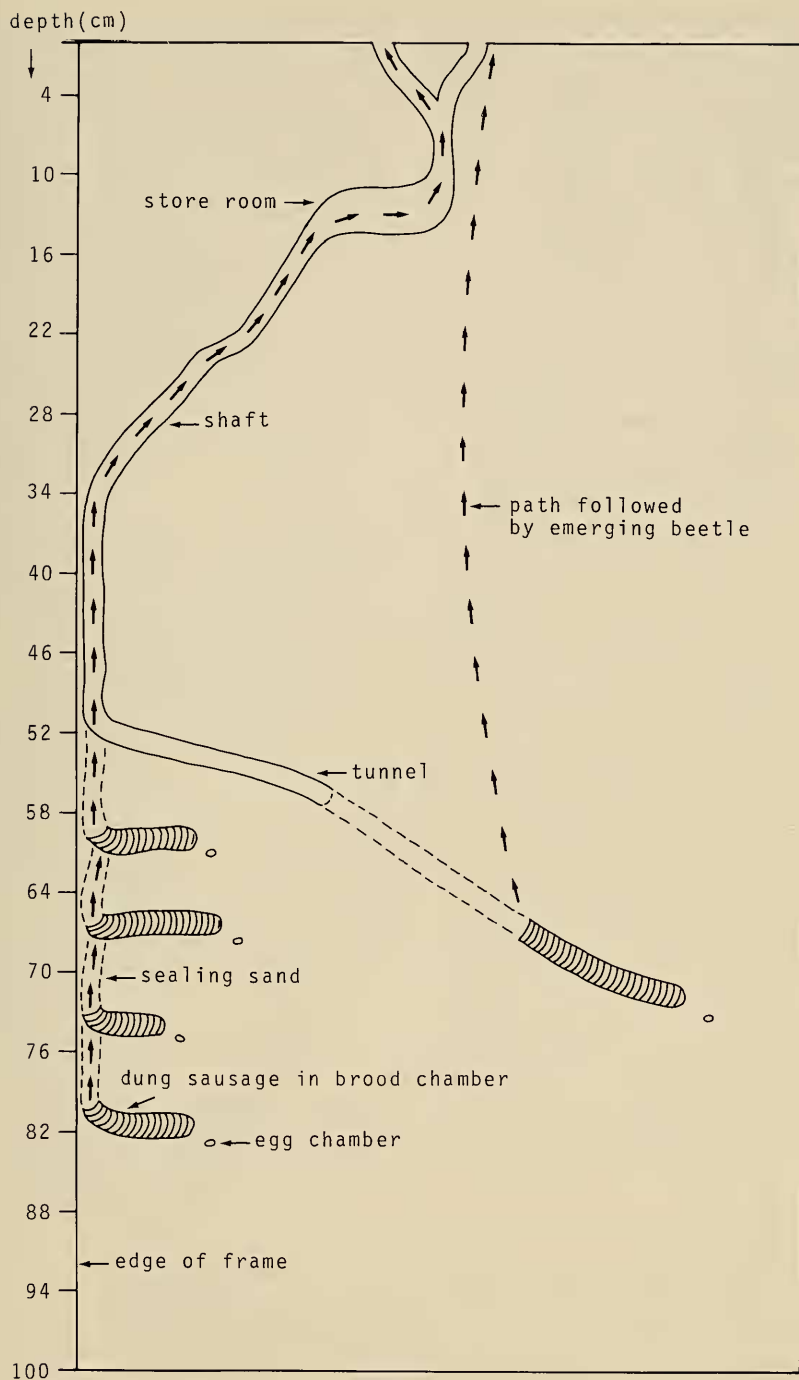
o ← egg chamber

← edge of frame

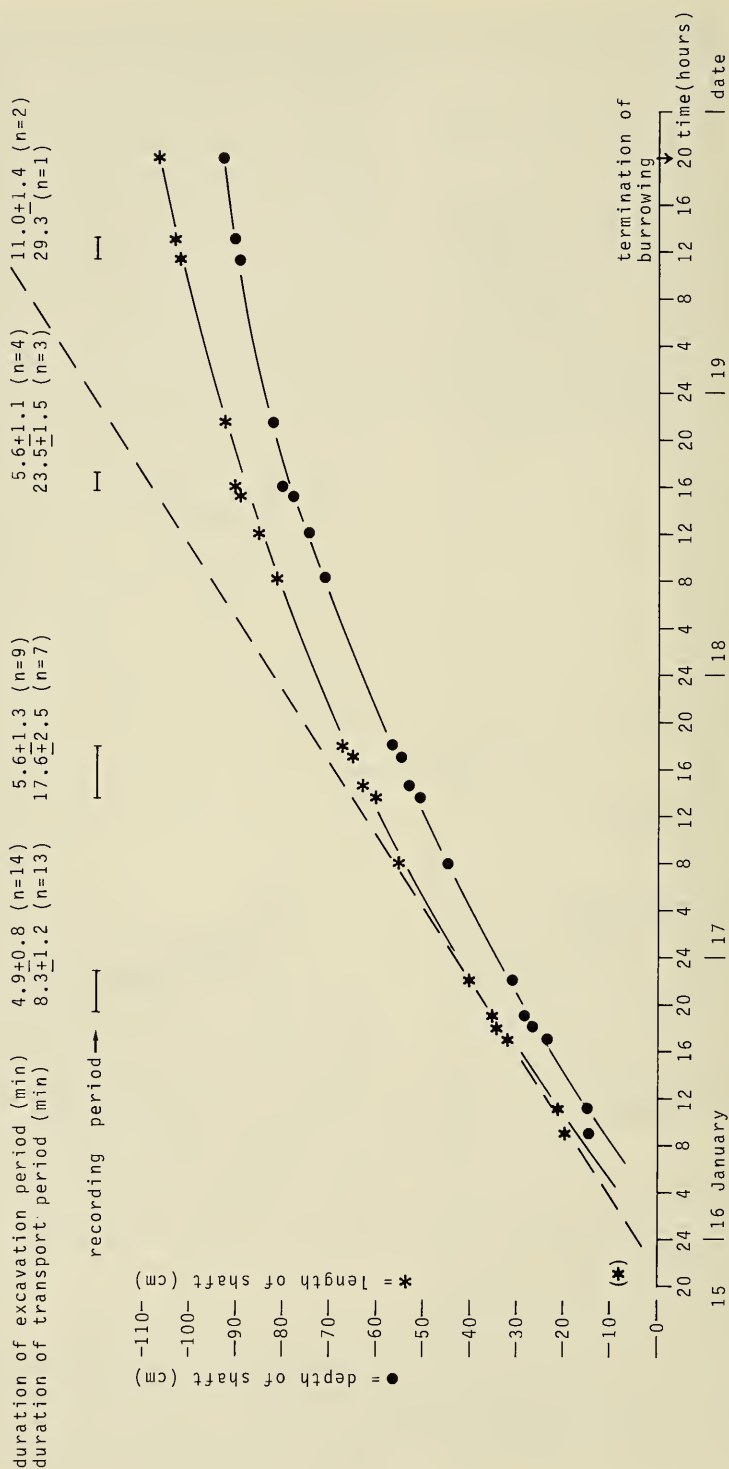Fig. 9. Nest of *Typhaeus typhoeus* in one of the glass cages.

Fig. 10. Sand excavation and transport at 5 °C by a pair of *Typhaeus typhoeus* in a glass cage filled with sand with a bulk density of 1.70 g/cm³.

rowing. The duration of sand transport steadily increased to half an hour per plug. The cage had been filled and the sand tamped down under water. This resulted in a bulk density of 1.70 g/cm³, which is the maximum a beetle may generally encounter in the field. The temperature in the room with the cage was 5 °C throughout the reproduction of the beetles. This approximates the soil temperature up to a depth of 1 m, measured in the field at the beginning of March, following the severe winter of 1978/79. This temperature was, therefore, near the lowest the beetles may encounter underground in the field in The Netherlands. Even so the beetles progressed fairly rapidly (fig. 10). In a total of 60 cages filled with less densely packed sand (not exceeding 1.55 g/cm³) and at temperatures of 5—17 °C the shaft was excavated within 1—3 days.

The morphology of the shaft was very variable. However, a horizontal part was invariably present within a depth of 30 cm. During the process of excavation the female often made another horizontal or slightly sloping gallery where she left the sand plug while continuing deeper. The shaft terminated in an oblique or horizontal gallery 6—15 cm long: the future first brood chamber (fig. 9). The depth of the shaft varied considerably, as can be seen from table 3.

The diameter of the shaft is determined by the size of the larger of the two beetles. In the field, casts of twelve shafts were made using liquid paraffin wax that solidified on cooling, enabling the diameter of the shafts to be measured. The mean diameters of all shafts were then averaged: the overall mean was 14.2 ± 0.7 mm (S.E.).

Oviposition and behaviour prior to and following it

As soon as the female has terminated the burrowing she begins to make a small cavity (diameter about 0.5 cm) for the future egg by moving her head and fore legs in the blind end of the almost horizontal terminal part of the burrow, alternately scraping some sand away and pushing part of it back. When she has finished she walks up and down the passage until the male arrives. The male joins the female, sometimes before she has finished the egg chamber, when he no longer encounters a sand plug to transport upwards. Then the beetles usually mate, as described before.

Copulation at this stage, i.e. prior to oviposition, is not obligatory but it is seldom omitted. After copulation the male starts scraping sand over a distance of about 10—15 cm from the bottom of the future first brood chamber. He may do this several times, so that a sand plug is formed. Then he turns around and transports the plug upwards. The female continues to prepare the egg chamber, breaking off to walk through the future brood chamber, with her abdomen pulsating. These pulsating movements are probably connected with the transport of an egg into the oviduct. Finally she moves her abdomen into the egg room and oviposits, making gentle pumping movements. Oviposition may last 10—25 minutes. After oviposition the female shows the backward scraping behaviour, just like the male, over a distance of some 10—15 cm, but in the opposite direction. Then she turns around and pushes the sand into the end of the burrow, thus sealing the egg chamber. The wall that thus separates the egg chamber from the future brood chamber becomes 10—15 mm thick (compare fig. 9). As a consequence of the scraping of sand by male and female the diameter of the brood chamber is slightly larger than that of the rest of the burrow: 15.0 ± 0.7 mm (S.E.), n = 12.

While the female is completing the egg chamber and preparing the brood chamber, the male is involved in widening the shallow horizontal part of the burrow, which is to become a store room for dung pellets. The diameter of the store room becomes 2—4 cm.

Table 3. Depth of shaft in *Typhaeus typhoeus* under laboratory and field conditions. [Temperature in the lab 5° or 9 °C; bulk density in glass cages and casks about 1.55 g/cm³ to match field conditions. Enclosures 1 × 1 m²; casks 0.5 × 0.5 × 1 m³. Ample supplies of dung were provided in all experiments.]

year	experimental set-up			n	depth (cm)	range (cm)
1979	glass cages	lab	(2-dim.)	12	67 ± 22	29—100
1979	enclosures	field	(3-dim.)	5	69 ± 6	63— 80
1980	glass cages	field	(2-dim.)	5	68 ± 9	52— 78
1980	casks	lab	(3-dim.)	4	58 ± 13	46— 78

Dung provisioning

When she has finished preparing the brood chamber the female walks up the burrow to meet the male in the store room or, alternatively, if he is ready first, the male walks down after enlarging the store room. When they meet, the female pushes the male upwards firmly and vigorously sweeps his elytra with her fore legs. This continues, until the male finally makes for the surface to fetch dung, the female waiting for him in the store room or in the brood chamber.

When he has found a fecal pellet, the male usually takes it between his front tibiae and walks backwards with it to the nest entrance. Sometimes he holds the pellet between his mandibles, but I have never observed the pellet being carried on the horns as described by Fabre (± 1910). The male drags the dung pellet into the direction of the nest entrance in a straight line, however tortuous his searching path may have been. If the dung pellet is found within about 40 cm from the nest entrance the male usually enters the hole at once. If the fecal pellet is found further away, however, the beetle drops it within 5—10 cm from the entrance and then moves directly to the entrance, walking forwards, puts his head into the entrance for a few seconds, turns around, picks up the dung pellet and carries it down without further delay. Whenever the beetle misses the entrance he finds it after an area-restricted search. This behaviour of searching for the entrance in the vicinity of the nest shows that the beetle is capable of roughly estimating the distance from the place where the dung was found. During the procedure of dragging a dung pellet from a fair distance away, the behaviour of leaving it behind and walking forwards to the nest entrance may occur more than once.

As soon as the male, dragging the dung pellet backwards into the nest, appears in front of the female below, she immediately begins to sweep his elytra. Then the male pushes the dung pellet underneath himself and walks up the shaft again to fetch more dung. The number of rabbit dung pellets dragged in successively by the male does not usually exceed 30; it depends on the ease with which he can find them and the distance to be covered. The time needed to collect them also varies, but seldom exceeds two hours. After this bout of dragging dung pellets, the male stays below-ground for some hours.

The female takes a dung pellet from the store room and, holding it in her fore legs, lets herself fall down the shaft by drawing in her middle and hind legs close along the body. In the brood chamber she tears the pellet to pieces with the help of her mandibles and fore legs and then firmly presses the pieces into the blind end of the brood chamber with her head and thorax, intermittently turning around her length axis. This firm pressing causes a meniscate layering within the dung sausage that is going to fill the brood chamber. The female walks up the shaft to collect every dung pellet. Alternatively, the male may supply her with dung by carrying down a number of fecal pellets. Sometimes the male kicks the dung pellets out of the store room with his hind legs. As a consequence the lowest part of the burrow behind the female becomes filled with fecal pellets.

Often, the male walks down the shaft to the female. If the female progresses too slowly he may stimulate her and he often tries to copulate. When the female goes up to fetch more dung to provision the brood chamber and encounters the male before she reaches one of the pellets in the store room, she invariably stimulates him by sweeping his elytra. It thus appears that the cooperation of male and female in the stage of dung provisioning is often reset by interaction.

The number of rabbit dung pellets processed per dung sausage varies between 30 and 65, averaging about 40. The number of dung sausages manufactured varies between 4 and 21, averaging about 10 (table 4).

Sealing the dung sausage and excavating the next brood chamber

When the dung sausage is finished the female

Table 4. Number of eggs laid (= dung sausages manufactured) in *Typhaeus typhoeus* under laboratory and field conditions. [Experimental conditions as mentioned in table 3.]

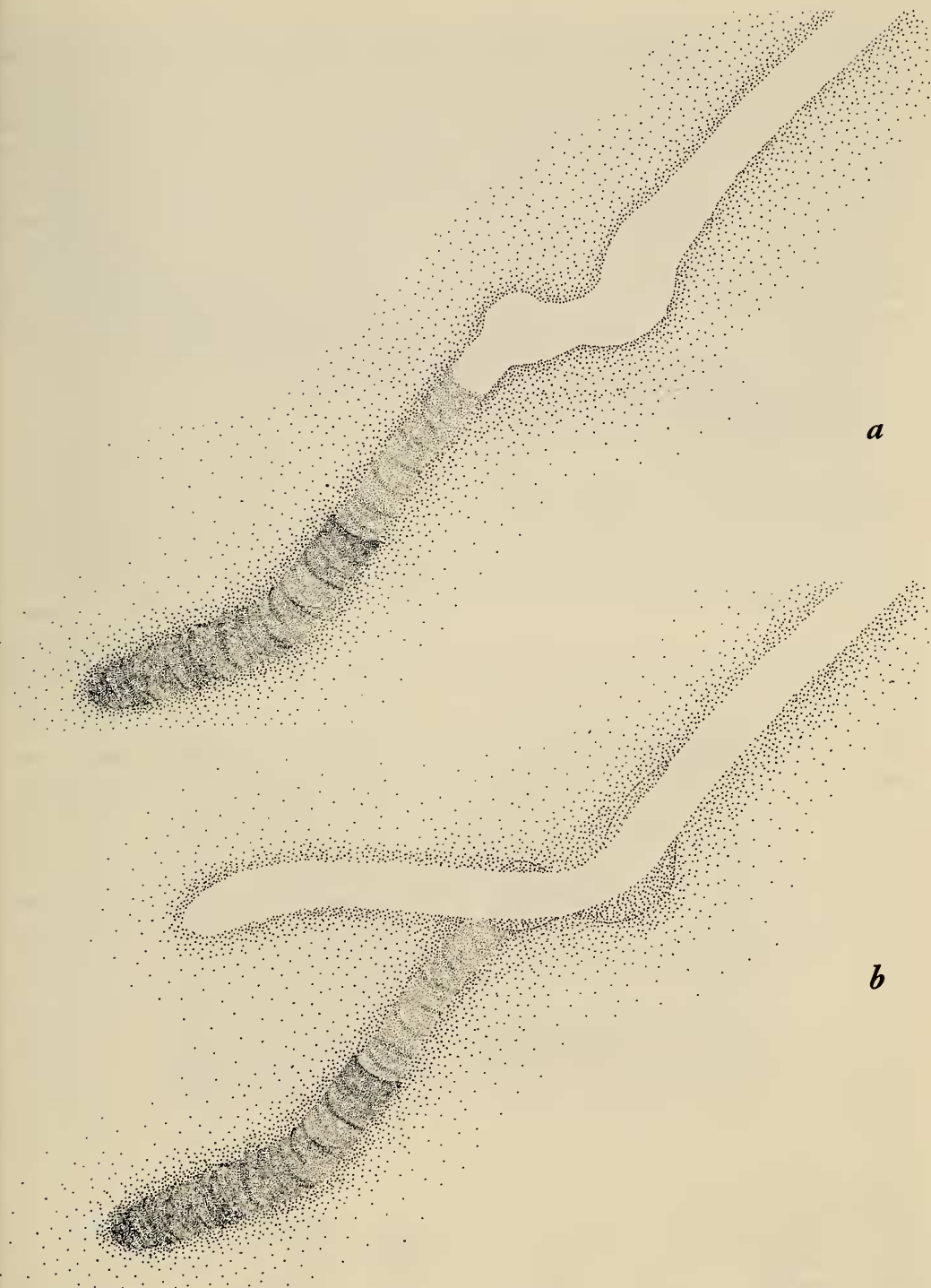| year	experimental set-up			n	number	range
1979	glass cages	lab	(2-dim.)	11	9.9 ± 4.3	5—21
1979	enclosures	field	(3-dim.)	5	10.6 ± 4.9	6—19
1980	glass cages	field	(2-dim.)	5	7.8 ± 2.9	4—12
1980	casks	lab	(3-dim.)	4	10.5 ± 1.7	8—12

Fig. 11a. Dung sausage being sealed over a predetermined stretch with sand from the shaft walls. Fig. 11b. The widening is plastered with sand from the new brood chamber.

seals it with soil, using sand scraped from the wall of the shaft. Interestingly, this wall-scraping starts some cm above the proximal end of the dung sausage and in this way the amount of the shaft to be filled with sand is determined (fig. 11a). Only half way or later in the stage of sealing is the next brood chamber excavated. The widened part of the shaft above the sand plug that seals the former dung sausage is inadvertently plastered by the beetle with sand that it drops as it is carrying it upwards (fig. 11b). The next brood chamber is excavated above the former one (fig. 12).

```
                    29 glass cages
                   /            \
5 with only 1 tunnel        24 with >1 tunnel
                              /          |
1 with the deepest        23 with the deepest
   tunnel not excavated      tunnel excavated
   first                     first
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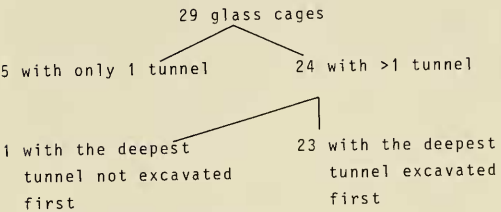
Fig. 12. Brood chambers are excavated above each other, beginning with the deepest.

Fig. 15 shows that the first tunnel excavated is usually the deepest. A tunnel is that part of the burrow from which one or more brood chambers branch off. This may be equivalent to a shaft, but more than one tunnel may be found branching off from the same shaft (fig. 9). A new tunnel is usually branched off when the latest brood chamber is relatively shallow. In the present study, the uppermost dung sausage in 22 cases with more than one tunnel was, on average, about 40 cm deep (table 5). While excavating the subsequent brood chambers the same behavioural sequence of transporting sand, copulation, oviposition and dung provisioning is shown.

As long as the male is present the female always excavates a new brood chamber, at times preceded by a new tunnel, irrespective of the availability of dung or the number of eggs already laid. If the male is no longer there, the be-

haviour of the female varies. If there is still a supply of dung she may continue the whole process of excavating a brood chamber, egg-laying, gathering dung and manufacturing dung sausages on her own. She may even excavate the next brood chamber with no male present and no dung around. If she has laid the next egg although there is no supply of dung, she may fill the newly excavated brood chamber with sand from the walls of the burrow, which shows that the behaviour after oviposition is fixed upon provisioning with whatever material there is around. Alternatively, the female may abandon the nest, invariably after finishing and sealing the last dung sausage, and continue reproduction elsewhere.

Behaviour of larvae and newly hatched adults

As soon as the egg has hatched the larva makes its way through the 1—1.5 cm thick sand wall that separates it from the dung sausage and moves into the dung in a somersaulting motion by which it displaces material from in front of it to behind it. As a consequence, after the larva has passed through, a small wad of dung, several mm long and wide, remains at the distal end of the dung sausage. The larva eats its way through the dung sausage, back-filling the space behind it with its excrement (fig. 13), so that the cavity surrounding the larva becomes only 2—3 cm long. It may eat its way through the dung sausage several times. There are three larval stages. Finally the larva III moves out of the dung sausage at the distal end and makes a cavity at the site of the former egg chamber: the pupal chamber. As a consequence, the distal end of the dung sausage becomes filled with sand displaced by the larva. The pupal chamber is plastered with excrement by the larva, which finally lies on its back to pupate (fig. 14).

After pupation the newly hatched adult often remains days or weeks in the pupal chamber before going to the surface. In my rearing trials, 45 out of 51 emerged adults passed through the partly eaten dung sausage, which thus appeared to be the rule. The other 6 immediately bur-

Table 5. Depth of uppermost dung sausage in shafts with more than one tunnel. [Experimental conditions as mentioned in table 3.]

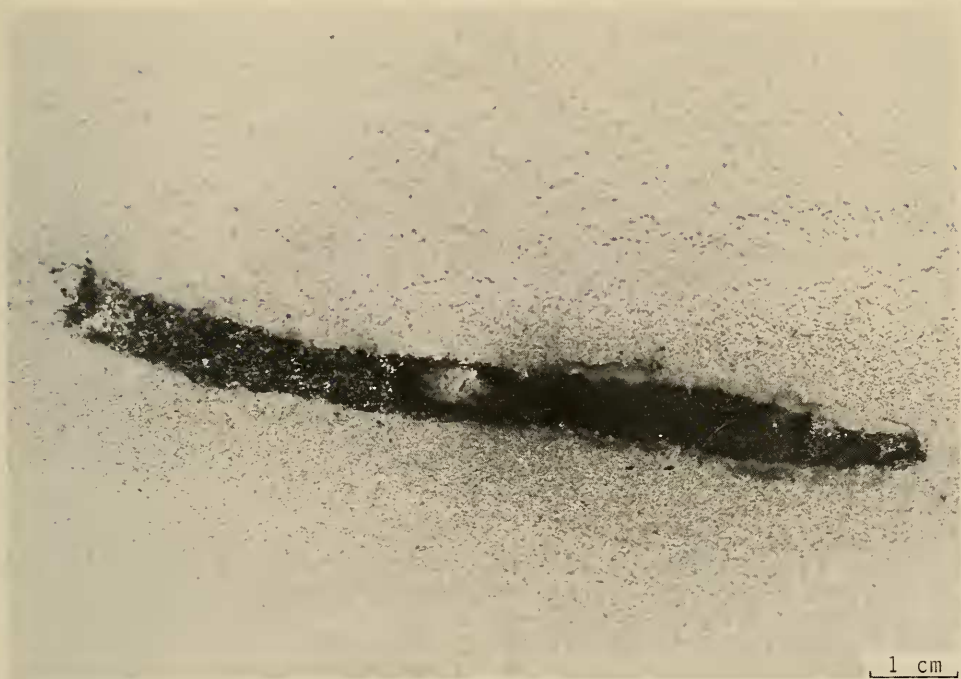| year	experimental set-up			n	depth (cm)	range (cm)
1979	glass cages	lab	(2-dim.)	10	36 ± 10	20 —48
1979	enclosures	field	(3-dim.)	5	42 ± 12	35 —54
1980	glass cages	field	(2-dim.)	3	38 ± 10	25 —50
1980	casks	lab	(3-dim.)	4	32 ± 8	20.5—40.5

Fig. 13. Larva of *Typhaeus typhoeus* eating its way from the distal end (right) to the proximal end (left) of a dung sausage and back-filling it with its own excrement. (Photo of dung sausage and larva in glass cage.)

Fig. 14. Pupa of *Typhaeus typhoeus* in pupal chamber made outside the distal end of the dung sausage. The horn (right upper part of pupa) shows that this specimen will become a male. (Photo of pupa in glass cage.)

rowed their own way upwards from the pupal chamber. At least 23 out of the 45 passing through the old dung sausage subsequently also burrowed their own way upwards. I believe this to be the normal behaviour because after passing through the old dung sausage, the remaining 22 broke through the sealing sand and subsequently followed the old shaft, but they were most probably forced to do so by the cages, so this should be regarded as abnormal behaviour (see the arrows in fig. 9).
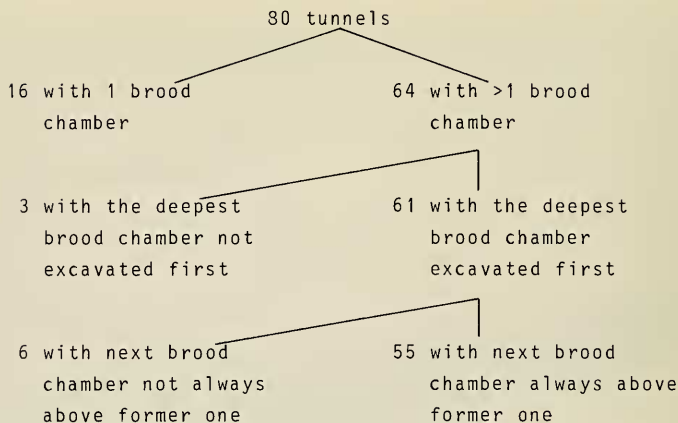
A beetle burrowing its way upwards scrapes.

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                              80 tunnels
                         _____/_____
                        /                  \
     16 with 1 brood                          64 with >1 brood
        chamber                                  chamber
                                    _____/|
                                   /                  |
      3 with the deepest                          61 with the deepest
        brood chamber not                            brood chamber
        excavated first                              excavated first
                              _____/|
                             /                     |
      6 with next brood                          55 with next brood
        chamber not always                          chamber always above
        above former one                            former one
```

Fig. 15. The tunnel excavated first is usually the deepest.

the sand away above itself, turns around and firmly presses it behind. Consequently, at the beginning of this behaviour the space in the old dung sausage or in the pupal chamber is filled with sand. Subsequently, a corridor about 8 cm long steadily extends upwards through the soil, the beetle scraping sand away above and pressing it beneath itself. An emerging beetle reaches the surface within a few hours, depending on the depth from which it starts. On arrival at the surface the animal shows the behaviour as described in the section on emergence and maturation feeding.

Development

Development of eggs and larvae

To study the (rate of) development of the different stages of *T. typhoeus*, beetles were reared in cages as described in the section on methods. The results of the rearing trials, which lasted almost three years, are given in tables 6 & 7, which cover the rearing period from winter 1979 to autumn 1980 and from autumn 1980 to autumn 1981, respectively. In the rearing trials the effect of administering cold winter periods was most noticeable. These cold periods were administered because soil temperature had been found to drop from 13 °C in August to 3 °C in February at a depth of 1 m in the field. At 0.20 m from the surface the fall in temperature was greater (from 16° to 1 °C).

After presenting the results of the rearing trials in the laboratory, the development of larvae in the field will be described. To facilitate com-

prehension, the course of development is briefly outlined in fig. 16.

Rearing trials (1979—1980)

The rearing trials were carried out in rooms with constant temperatures of 1°, 5°, 9°, 13° and 17 °C, respectively. These temperatures were chosen because soil temperatures measured in 1979 in the study plot at Wijster (where *T. typhoeus* occurs naturally) ranged from 3—10 °C in the reproductive period and increased to 13—16 °C during summer, when the larvae develop. At all the temperatures they were subjected to, the beetles showed their reproductive behaviour.

At 1 °C only very few eggs were laid, however, and the dung sausages were abnormal, consisting partly or completely of whole dung pellets. The eggs did not hatch. Therefore the rearing trials carried out at 1 °C will not be discussed further. At 5 °C reproductive behaviour was normal, but the eggs did not hatch either, not even after 20 months. At a temperature at or exceeding 9 °C the eggs did hatch. The time eggs laid at 5 °C took to hatch at 9°, 13°, 17° and 20 °C was estimated (table 8). Though the number of observations is small in some groups (because this trial was not solely intended to study the hatching time of the eggs) it is quite clear that at 9 °C development is relatively slow. At the start of the rearing trials there were four cages at each temperature. However, three of the cages kept at 9 °C soon had to be discarded because in one cage the female died without reproducing and although

Table 6. Results of rearing pairs of *Typhaeus typhoeus* in glass cages at four different temperatures.

1) Stopped in November 1980, i.e. 20 months after the start.
2) Initially 4 pairs of beetles, soon declining to 1 pair, see text.
3) Artificial winter period at 5 °C from 5 XI 1980 to 23 I 1981, i.e. 11 weeks.
4) Stopped in September 1981, i.e. 20 months after the start.

Data from pairs subjected to a cold period from 30 October 1979 to 28 February 1980 are presented on the right side of the relevant columns; data from pairs not subjected to a cold spell are given on the left side. Totals at the bottom of the table pertain to data from rearing trials at 13° at 17 °C only (see text), hence the break in the table between the 9° and 13 °C rows. There was a significant difference between the number of beetles that emerged from the cages receiving a cold treatment and those that emerged from the cages that did not receive a cold treatment: $\chi^2 = 21.85^{***}$.

Table 7. Results of ongoing rearing trials in glass cages from November 1980 until October 1981 in rooms kept at a temperature of 13° or 17 °C.

winter periods offered at 5 °C as indicated in Fig. 12		number of pairs of beetles	number of pupal chambers on 5 November 1980	number of pupal chambers on 1 July 1981	number of pupal beetles that emerged in 1981	number of pupal chamber, not pupating	larvae remaining in pupal chamber, living	number of cold period and cages not given a cold treatment	difference in number of beetles that emerged from cages	sex ratio of emerging beetles (females : males)
-	+	7	27	27	23	0				
+	+	7	2	+4 = 6	5	0			$\chi^2 = 20.12***$ (P << 0.005)	18 : 15
+	-	6	6	+1 = 7	0	2				
-	-	7	11	+3 = 14	5	8				

five dung sausages were made in each of the other two cages they were very superficial and the larvae soon died, probably because the fluctuations in moisture were too great.

On 30 October 1979, by which time virtually all the larvae had emerged, the cages were divided into two groups, one group remaining at the temperature it had been subjected to so far, the second group receiving a five-month cold spell at 5 °C until 28 February 1980, after which the cages were once again subjected to their former temperatures. The single cage remaining at 9 °C was assigned by chance not to receive a cold spell. One year later, rearing at 9 °C was repeated with one cage that was given a cold period (see table 6). The number of pupal chambers and the time that elapsed until they appeared can be read from table 6. At 9 °C the median number of pupal chambers was reached much later in the cage without a cold period than in the cages at 13 °C and 17 °C, whether or not the latter received the five-month cold spell. This

again indicates that development is very slow at 9 °C.

At 13 °C and 17 °C pupal chambers were made by the larvae of all groups. This proves that a cold period is not a prerequisite for making a pupal chamber. At 13 °C and 17 °C, in the groups receiving a cold period, the median number of pupal chambers was achieved after a similar period from the start of the trials: 55 and 52 weeks, respectively. The date by which half the beetles had emerged was also very similar for these two groups. Therefore, I felt justified in combining the data on the different stages in the cages kept at 13 °C and 17 °C (bottom of table 6). This resulted in a very significant difference between the proportions of beetles emerging from cages which had and those emerging from cages which had not been subjected to a cold period: only one beetle emerged from 19 pupal chambers in the latter, compared with twelve beetles out of 14 pupal chambers in the former ($\chi^2 = 21.85***$, P << 0.005). Thus a
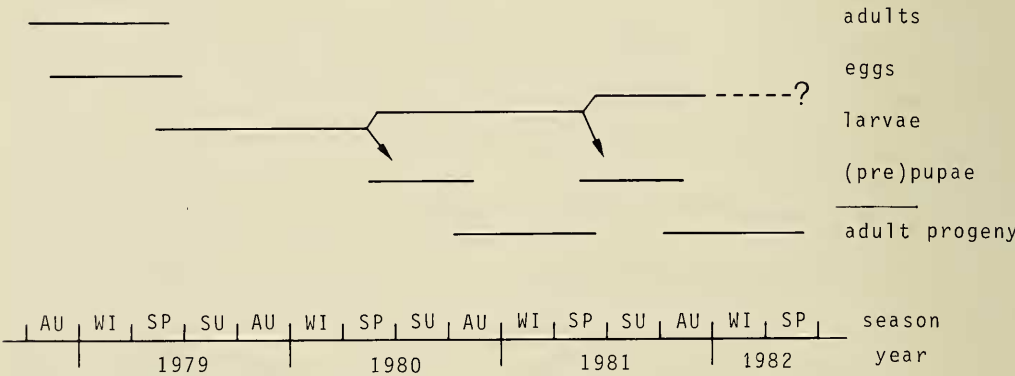

Fig. 16. Outline of development of life stages in *Typhaeus typhoeus*. At the bifurcations arrows indicate larvae changing into the pupal stage, while the continuous line indicates remaining in the larval stage.

Table 8. Numbers of eggs hatching and median time that elapsed before hatching in a rearing trial in glass tubes.

temperature (°C)	number of glass tubes with egg and dung sausage at start on 28 August 1980	number of eggs that hatched / median number of eggs had hatched	number of weeks that elapsed until
9°	5	3	7 - 8
13°	44	39	3½
17°	5	3	2½ - 3
20°	5	3	2 - 2½

cold period, although not a prerequisite, certainly favours the completion of the life cycle. The single beetle that emerged from a cage without a cold spell appeared in the same period as those from the cages subjected to a cold interlude (table 6).

Of the 13 beetles that emerged, six were females and seven were males: a 1 : 1 sex ratio.

From these results it can be inferred that soil temperatures in the field ranging from 3—10 °C in early spring to 13—16 °C in summer, favour reproduction and the development of the larvae.

Two other experiments in cages were carried out in early spring 1979, one at 5 °C and one at 9 °C. These will be reported in another paper. In June 1979, when reproduction in these experiments was over, the cages were taken to rooms in which constant temperatures of 13 °C or 17 °C, respectively, were maintained. Thenceforth these cages were exposed to the same treatments as those in the above-mentioned rearing trials, including the division into groups that did or did not receive the cold period. Data on pupal chambers and the beetles that

emerged are given in table 9. The results clearly confirm the conclusions already reached regarding sex ratio and effect of a cold spell on rearing results.

Rearing trials continued (1980—1981)

As mentioned before, in cages at 5 °C, the eggs had not hatched after 20 months. The two cages at 9 °C, one of which had received a cold winter period, were kept at 9 °C until 20 months had elapsed from the start of the rearing trials. By that time they contained three and one live larvae in pupal chambers, respectively. It may thus be surmised that even at such a low temperature adult beetles might have emerged after a (new) cold period.

Since the results of the 13 °C and 17 °C treatments of the three trials were similar and, moreover, the beetles emerged in the same period (tables 6 & 9), those cages that apparently still contained life after the period of emergence of the beetles, were pooled and subsequently divided into four groups for continued rearing. Two of the groups were subjected to a cold period at 5 °C from 5 November 1980 to 23 January 1981. This was done in such a way that after the rearing trials were completed all four combinations of 0 to 2 cold periods had been realized, as outlined in fig. 17. The results are given in table 7.

A beetle emerged from almost all pupal chambers in cages subjected to a cold period for the first time (23 beetles out of 27 pupal chambers). In cages that had already received a cold period during the 1979—1980 part of the rearing trials, only two pupal chambers remained in which the larva had not pupated. During the 1980—1981 part of the rearing trials this small number rose to six and, when subjected to a second cold period, a beetle emerged from five of

Table 9. Rearing results from two additional experiments. Data on left of columns pertain to glass cages that had not received a cold period. Data on right of columns pertain to glass cages that did receive a cold period.

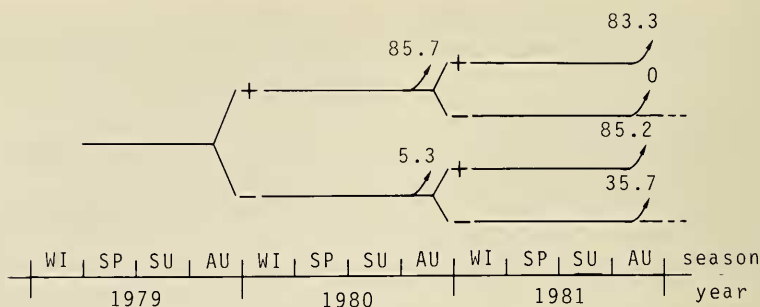|	number of pupal chambers	number of beetles that emerged	number of beetles emerged	first date with median number of beetles emerged	difference in number of beetles that emerged from glass cages receiving and not receiving a cold winter period	sex ratio of emerging beetles (females : males)
additional experiment (13°C)	15 / 27	0 / 27	- / 30 IX 1980	x² = 42.00*** (P << 0.005)	14 : 13
additional experiment (17°C)	8 / 9	2 / 9	25 IX 1980 / 25 IX 1980	x² = 10.43*** (P < 0.005)	5 : 6

Fig. 17. Cold spell at 5 °C (+) or no cold spell (−; constant temperature of 13 °C or 17 °C) administered in rearing trials during 1979—1981 and percentages of adults emerging. Percentages pertain to numbers mentioned in Table 6, columns 8 and 12, and Table 7, columns 4 and 5.

these six pupal chambers. But in the cages not subjected to a second cold period no beetles emerged from the seven pupal chambers. Few beetles emerged from cages that received no cold treatments (five beetles from 14 pupal chambers). As in 1979—1980, the number of beetles that emerged after a cold period during the 1980—1981 part of the rearing trials differed very significantly from the number that emerged from cages not subjected to a cold period ($\chi^2 = = 20.12^{***}$, P << 0.005).

Of the 33 beetles emerging from the cages in 1981, 18 were males and 15 females, which confirms the 1 : 1 sex ratio found the previous year. All twelve larvae remaining after the 1980—1981 part of the rearing trials were in their third instar (head capsules 4.6—5.2 mm).

Development of larvae in the field

Evidently, the quantity of cold that larvae of a given generation experience in the field during winter will differ because of the differing depths at which eggs are laid in the soil and because some winters are more severe than others. In general, the larvae occurring closest to the surface will experience more cold in winter and more heat in summer, which may accelerate their development vis-à-vis that of deeper larvae. To test this, five cages were dug into the soil in the study plot at Wijster in November 1979, in such a way that their upper edges just reached the surface.

At the beginning of March 1980 a pair of dung beetles and ample dung were introduced into each cage. The beetles were prevented from exchanging with the surrounding field population by wire-netting placed over the cages' walking surface. The cages were dug out at the

beginning of September 1981, by which time larvae that had completed their life cycle could be found as newly hatched but not yet emerged beetles; in addition, this was also the right time to check whether, as expected, some of the larvae had not yet completed their life cycle. The five cages proved to contain 39 dung sausages. In eleven of these a living larva was found, one of which was in a pupal chamber. All larvae were in the third instar (head capsules 4.5—5.0 mm). In addition, one newly hatched beetle was found. Though this is minimal evidence, the trial does demonstrate that under field conditions larvae of the same generation may give rise to adult beetles in different years, assuming, of course, that some of the remaining larvae would complete their life cycle in the future, as occurred in the laboratory rearing trials. Interestingly, the cage with the adult beetle also contained a larva in the pupal chamber and some other larvae, still in dung, which shows that different rates of development may occur in the offspring of one pair of beetles.

The results of another field trial, executed in the same period, enable a judgement to be made about whether the poor survival obtained in the above-mentioned field trial (life in 12 out of 39 cases = 31%) was somehow induced by the glass cages. In this trial five pairs of beetles were released in enclosures measuring 2 × 2 m², at the beginning of March 1980. Their nests were dug up in May and June 1981, i.e. about three months earlier than the cages. There proved to be 32 dung sausages, 14 of which (i.e. 44%) contained a living larva; three of them had already made a pupal chamber. Assuming some mortality in the enclosures between May/June and September, the data suggest that there was

no difference in survival between the enclosures and the cages. Thus there is no evidence that the cages have a detrimental effect on survival.

Conclusions on rearing

The results from the rearing trials imply that the development of the larvae is very slow at 9 °C as compared with that at 13° and 17 °C. The latter temperatures closely approximate those in soil during summer. Some larvae pass through the life cycle at constant high temperature (17 °C). But the proportion of larvae that develop into adults is greatly improved by a cold period in the third larval stage. This condition matches to a varying degree the low soil temperature during winter. Depending on the experience of a cold winter period, larvae of the same generation and even from the same pair of beetles may give rise to adults in different years. So the life cycle may last three instead of two years and perhaps even longer. This variation in the duration of the life cycle enables genetic exchange between reproductive pools to be passively achieved in successive years.

Longevity of adults

Genetic exchange between reproductive pools in successive years might also be achieved if adult beetles reproduced more than once. This is unlikely to be the case in *T. typhoeus*, since in all laboratory trials executed at a temperature above 5 °C and in all the field trials, the beetles died shortly after reproduction. In many insect species, the dissection of females starting repeated reproduction reveals the presence of yellow bodies (corpora lutea) at the terminal ends of the ovarioles; these are the remnants of the follicular epithelium, which degenerates after egg release (Krehan, 1970; Vlijm & Van Dijk, 1967). To investigate whether yellow bodies are formed and can be found in *T. typhoeus*, adult females were collected in the course of their active period and subsequently dissected. Moreover, females from several experiments that died after reproduction were dissected. Of 14 females that died after reproduction, three proved to possess corpora lutea. This indicates that in *T. typhoeus* yellow bodies are not always formed to an extent that they can be recognized. Of 52 females, captured in the field in the course of the season, eight possessed distinct corpora lutea and three only a vague indication of these. These eight females were captured late in the season (May and June). Obviously, it was not known whether these females were on their way to aestivate or to die.

Clearly, the absence of yellow bodies does not allow conclusions to be drawn about repeated reproduction, and only if their presence is established at the onset of the reproductive period can these bodies be used as indicators of repeated reproduction.

Therefore, an experimental approach was followed. A trial to have beetles aestivated and let them reproduce in the following activity period was executed twice. From May 1979 onwards, 60 beetles, captured when newly emerged in October and November 1978, were kept in plastic jars (13 cm deep, 10 cm in diameter; one beetle per jar) containing moist sand at a temperature equal to that measured in the study plot at Wijster 20 cm below the surface. Natural daylength was applied. The beetles were regularly supplied with fresh rabbit dung. Of the 60 beetles, 25 had survived after reproduction (13 males and 12 females) before May at a constant temperature of 5 °C. The other 35 (23 males and 12 females) had been kept at 5 °C in the jars since their capture. By 2 August 1979 all the beetles had died except for two males (one male from each group). Shortly thereafter the temperature-regulating equipment in the laboratory broke down and the beetles died from heat.

In 1980, 25 beetles that had not reproduced but that had been kept in plastic jars at 5 °C since their capture in autumn 1979 were used in a trial. No beetles that had already reproduced were available. In mid-March 1980 these 25 beetles were divided into four groups: staying at 5 °C (three males, one female); 9 °C (six males, three females); 13 °C (five males, one female); and 17 °C (five males, one female). By 1 July all the beetles kept at 9°, 13° and 17 °C had died; two males at 5 °C were still alive. These two males survived and were given the chance to pair with two fresh females in glass cages on 27/28 November 1980. One male died on 2 December without having reproduced, the other died on 15 December after the female had laid a few eggs.

From the results of the dissection and of the trials, it can be concluded that aestivation of adult beetles and repeated reproduction in *T. typhoeus* is very exceptional, if indeed it occurs. Most of the beetles die after the first reproductive season. Thus the contribution to genetic exchange between reproductive pools in successive years by means of survival of adults is virtually non-existent.

DISCUSSION

Influence of glass cages on behaviour and results of rearing

Although the behaviour of the beetles seemed normal, the narrow space in which they were confined may have influenced their behaviour. Tables 3 & 4 show that there were no major differences in the depth of the shaft and number of dung sausages between beetles kept in the laboratory and those kept or found in the field. Moreover, the number of dung sausages produced in the present trials was very comparable with figures reported in the literature (tables 2 & 4). As reported in the section on the development of eggs and larvae, the survival of larvae kept in glass cages dug into the soil and kept in enclosures in the field was similar. This confirms that glass cages do not adversely affect the behaviour of the beetles.

Pheromones

There are few data on settlement and pair formation in the literature. Halffter & Matthews (1966), in their extensive review of the biology of Scarabaeidae, assume that the sexes meet by chance near the dung patch. In addition to the case of *Typhaeus hiostius* mentioned earlier (Crovetti, 1971), the intrusion of a male into a female's feeding burrow and joint feeding until sexual maturity, is also reported by Rommel (1961) in *Copris hispanus* and by Halffter & Lopez (1977) in *Phanaeus daphnis*. The hypothesis of pheromone communication in *T. typhoeus*, tentatively suggested in the present paper, is supported by reports that in Scarabaeidae some dung patches are densely populated with beetles, whereas others are not, and that the densely populated dung patches often differ from each other in the taxon that is most represented (e.g. Halffter & Matthews, 1966; Paschalidis, 1974). A similar clustered distribution is known in bark beetles (Scolytidae), and this is known to be caused by aggregation pheromones (Blight et al., 1980). By analogy, pheromones may be important in dung beetles, too. Moreover, the stance adopted by the male *T. typhoeus* during the supposed pheromone release is virtually the same as that described by Paschalidis (1974) in three scarabaeid *Sisyphus* spp. and by Tribe (1975) in *Kheper nigroaeneus*. In the latter case pheromone release was proved. In *Kheper* the pheromone is released from a depression on either side of the first abdominal sternite, with the help of paraffin tubules as a carrier. This is very different from the way the pheromone is supposed to be released by *T. typhoeus*, i.e. along with the excrement. The latter mechanism is also known for other groups, e.g. in bark beetles, boll weevils and some Orthoptera (Jacobson, 1972). If properly supported by additional research, pheromone release by *T. typhoeus* would constitute the first known example of pheromone communication in Geotrupidae. The conformity in releasing stance and the difference in releasing mechanism point to a convergent development and may be added to arguments in favour of the modern view of classifying scarabaeids and geotrupids in distinct families (Crowson, 1967, 1981) instead of in subfamilies (Halffter & Matthews, 1966).

In all cases the pheromone release stance has so far only been described in male dung beetles. The possibility should not be excluded, however, that after maturation feeding the male is also attracted to his first female by means of pheromones. Fabre (± 1910) had already noticed that at times two or three males of *T. typhoeus* can be found in a burrow with only one female. Teichert (1955) observed the same in *G. mutator* and from this he inferred that males were attracted by pheromones released by the female. This would certainly improve the female's chances of mating. It has been stated by Halffter & Matthews (1966) that the similar size of the antennal clubs in almost all male and female dung beetle species is a sign of the unimportance of pheromone communication in these beetles. But this argument does not hold if both sexes respond to pheromones.

Burrowing

One may wonder how much faster the female progresses in the burrowing stage thanks to help from the male. The gain is estimated by Teichert (1957) to be one-fourth to one-third of the excavation time.

Co-operation between male and female in the burrowing phase is not so close in some species as it is in *T. typhoeus*. It is marked in the relatively deep burrowing species *Geotrupes vernalis*, *Lethrus apterus* and *Typhaeus hiostius*, whereas in the shallow burrowing species *G. mutator*, *G. stercorarius* and *G. spiniger* the male does little more than remove some soil from the entrance (Teichert, 1955, 1959a, 1959b; Crovetti, 1971).

According to Klemperer (1979), in *G. spiniger* the female stops excavating the shaft and the brood chamber as a response to their length.

Behaviour preceding and following oviposition

Oviposition in *T. typhoeus* is almost always preceded by copulation. According to Weaver & Pratt (1977) repeated copulation has a stimulating influence on the reproductive effort in the cockroach *Periplaneta americana*. This is probably why a female of *T. typhoeus* that has lost the male continues reproduction much more slowly.

During the backward scraping activity that follows oviposition, the beetle presses its head and thorax hard against the walls of the brood chamber, possibly to make the walls resist the pressure they will be subjected to when being provisioned with dung. Although he did not observe the pressing behaviour, Fabre (± 1910) noticed that the walls of the brood chamber were smoother than those of the shaft.

Dung provisioning

One may wonder how the male orients himself on the surface, when dragging a dung pellet to the nest entrance. Kuyten carried out some unpublished experiments in 1961/62 from which he concluded that the position of a light source provides the beetle with a directional cue. The same conclusion was independently reached by Frantsevich et al. (1977) after some very similar experiments with *Lethrus apterus*. But it has not yet been explained how *typhoeus* takes its bearings by night or on cloudy days, when most of the excursions for dung are made.

Sealing and excavating brood chambers

Klemperer (1979) states that in *Geotrupes spiniger* sealing a dung sausage is a side-effect of excavating the next brood chamber. In *Typhaeus typhoeus*, however, at the start of sealing the sand is scraped from the wall and firmly pressed into the shaft above the dung sausage. Moreover, the last dung sausage is invariably sealed; this is also evidence of a distinct behavioural phase.

In the endemic Sardinian species *Typhaeus hiostius*, which closely resembles *typhoeus* both in its biology and in the reproductive season, the sequence of excavation of brood chambers is remarkably different. Contrary to *typhoeus*, *hiostius* constructs the uppermost dung sausage first, at about 60—70 cm below the surface, and every subsequent sausage is 10—15 cm deeper, the completed burrow generally reaching a depth of 1.30—1.60 m. As a result, under field conditions some weeks after the nest has been completed the uppermost dung sausage already contains a larva III, whereas the egg belonging to the lowest dung sausage has not yet hatched (Crovetti, 1971). This behavioural sequence may well be related to soil moisture conditions (Crovetti, pers. comm., 1981), the female beginning to lay eggs approximately at ground-water level and then deeper as the water table falls. The ultimate function of this sequence may be to ensure that eggs and larvae do not dry out during the hot summer.

In *T. typhoeus*, however, the risk of drying out may be considerably lower. In this species, laying the first egg approximately at ground-water level and thenceforth more shallowly may ensure that the larvae and their dung sausages do not become waterlogged during the next winter. In this context it would be interesting to study the behavioural sequence in *typhoeus* in the southern part of its geographical range.

Emergence through soil

The way the beetle moves to the surface is seldom mentioned in the literature. Sano (1915/16) reports that *Geotrupes stercorarius* does not always use the original tube made by the parents, but makes its own route, as described for *Typhaeus typhoeus* in this paper. Crovetti (1971) reports that *T. hiostius* breaks through the partly eaten dung sausage and the sand that seals it and follows the shaft made by the parents. The evidence available for *T. typhoeus* (this paper) and for *T. hiostius*, suggests that the newly hatched beetle starts moving upwards at a place where the resistance from soil is least, i.e. through the remnants of the dung sausage. However, it seems to be luck, rather than strategy, whenever the beetle finds the open part of the parental shaft. Emergence through soil thus seems to be the rule.

Behaviour as a reaction chain

According to Klemperer (1979) the nesting behaviour of *Geotrupes spiniger* can be described as a reaction chain in which each action generates its own terminating stimulus and initiates the subsequent response. Although experimental analysis is beyond the scope of the present paper, the nesting behaviour of *T. typhoeus* is in many respects very similar to that of *G. spiniger*. In addition, the way in which the stretch of the burrow that is to be filled with sealing sand is determined in *T. typhoeus* (fig. 11) is an example of an action that generates its own terminating stimulus. So it may well

be that the behaviour of *typhoeus* can also be described as a reaction chain. The extent to which signalling between the sexes by means of pheromones, sweeping each other and stridulation alters this picture requires further research, however.

The role of temperature in diapause and development

Diapause is induced in the third larval instar and can be overcome by a cold winter period at 5 °C. Tauber & Tauber (1976) rightly point out that this does not prove that diapause develops under the influence of low temperature in nature, as in many instances diapause can artificially be broken in several ways, including manipulation of day-length and administering a high temperature. Yet it is difficult to imagine an environmental stimulus other than temperature that would induce, maintain and develop the diapause in larval dung beetles, since they live in complete darkness and in well-drained soils in which, over the year, differences in moisture are rather unpredictable. On the other hand, although temperature is known to be the single environmental stimulus maintaining rhythms in a number of insects during the day (Saunders, 1976), total reliance on temperature as a diapause-regulating factor in the course of the year has, to date, only been reported in tropical insects (Tauber & Tauber, 1976).

Regarding the role of temperature in larval development, the few larvae that deviated from the general pattern in the rearing trials (tables 6 & 7) are interesting. Some larvae did not complete their life cycle after a cold period. This suggests there may be considerable variation in the amount of cold (duration and/or degree) a larva needs before diapause is terminated. On the other hand, some larvae completed their life cycle without a cold interlude. As the latter were from the cages kept at 17 °C this suggests that a relatively high temperature can also overcome diapause. Raising the temperature from 15° to 21 °C has, for example, been shown to be sufficient to overcome diapause in rearing trials of *Geotrupes spiniger* (CSIRO, 1980: 66). This should be further studied in *T. typhoeus*, since it may mean that in the southern part of the geographical range a warm period in the first summer (summer 1979 in fig. 16) may be sufficient to enable the species to pass through its life cycle within one year. This may help to explain why Fabre (± 1910), working in southern France, found a one-year life cycle in his first

rearing trial (though not in his second). The same phenomenon may occasionally occur in the northern part of the geographical range too, e.g. in a hot summer, but as a rule in those regions development will continue after a cold period in winter (winter 1980 in fig. 16), which thus leads to a life cycle of a minimum of two years. Spaney's suggestion (1910) (he worked in Germany) that in most cases *T. typhoeus* has a one-year life cycle, should be regarded with suspicion. Main (1916/17), working in England, found a two-year cycle. Though most Geotrupidae have a one-year life cycle, some are known to show a cycle of at least two years (Sano, 1915/16; Main, 1916/17; Howden, 1955).

Field results support the hypothesis that larvae of the same generation develop at different rates: the rearing trial in glass cages, dug into the soil and started in March 1980, yielded one adult beetle and a number of larvae in their final instar in the autumn of 1981 (see section Development, p. 224). But as only one adult beetle emerged, the hypothesis that the rate of development is related, by means of temperature, to the depth at which the larvae develop, could not be tested.

Regarding the development of eggs laid before the turn of the year, it is unlikely that these eggs can hatch before winter, let alone reach the third larval stage, since soil temperature at 20 cm to 100 cm below the surface is uniformly ± 9 °C by late October and subsequently decreases. As a consequence, the eggs do not hatch until early spring together with the eggs laid by that time, and the larvae do not experience a cold spell until the following winter. It may thus be inferred that a one-year life cycle probably cannot be achieved in The Netherlands, starting from these early eggs. This may not be true, however, in the southern part of the geographical range.

Flying

The Geotrupidae differ greatly in their use of flight. As early as 1910, Spaney remarked that *Geotrupes stercorosus* and *Typhaeus typhoeus* can rarely be observed flying, whereas *G. stercorarius* regularly flies. He thought this was because beetles of the first two species generally find plenty of food around in the place where they emerge and reproduce, whereas those of the last need to move from one fresh dung source to another. As regards the significance of the flying behaviour in the life history of *T. typhoeus*, three observations seem to be relevant.

First, the behaviour is shown in the laboratory in the presence of an ample supply of dung. Second, most of the beetles captured flying in the field did not have an empty gut. And third, I have observed the flying behaviour in the field in places with adequate supplies of dung that are apparently easily accessible to the beetles. This shows that flying is not solely connected with a shortage of dung and it may well be that flying is mainly related with searching for a partner. At the end of the season, however, there may be less dung available because it has been used by the beetles and because the density of the rabbit population has decreased, and then the beetles may fly in search of new dung supplies. This aspect needs to be studied further.

Persistence of populations in space and time

Clearly, much speculation remains about the cause and function of flying in adult *T. typhoeus*. There is also speculation about the selective forces that have led to and maintain the pronounced differences, both within and between pairs of reproducing beetles, in the depth at which the eggs are laid. Ignoring the causes, the different rates of development of larvae from one generation lead adult beetles to emerge in different years; this passively contributes to a reduction of the risk of local population extinction in time. Similarly, the dispersal of adults results in, although is not necessarily aimed at, reducing the risk of local population extinction in space (Den Boer, 1968). The extent to which these phenomena contribute to the persistence of *T. typhoeus* populations within a certain area merits further study.

OUTLOOK

The present investigation of the biology of *Typhaeus typhoeus* will prove to be invaluable for the follow-up studies. Among the most important findings for the understanding of soil morphology and soil formation are: first, the observations of how, and to what extent, the burrows are excavated and, in particular, subsequently back-filled with dung and soil; and, second, the way in which newly hatched adult beetles make their way to the surface.

For the understanding of environmental factors (including soil conditions) that play a role in the species' burrowing behaviour and reproductive performance, results of rearing trials will prove indispensable.

Apart from these aspects, which are closely related to the soil-oriented approach of the study, the present investigation reveals a number of starting points that may also be worth developing. The co-operation between male and female is so striking that further study is promising both from an ecological point of view (what is the gain in time and energy for the female and in net reproduction for both partners?) and, if carried out as a comparative study of related species, from an evolutionary point of view (how and when did co-operation develop?). In addition, the role of contests and the probable role of pheromones deserve further study, both in pair formation and in the exploitation of food resources. These aspects, pheromones and co-operation (and concomitant interaction) between the sexes, may reveal new insights in future ethological analyses of the nesting behaviour of dung beetles. Finally, a long-term study may reveal how much the differential development time of larvae and the dispersal of adults contribute to reducing the risk of local population extinction and to stabilizing beetle numbers.

Such studies may reveal the adaptive value of numerous aspects of dung beetle behaviour, about which we can only speculate at present.

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